

Effects of single-tree selection harvesting on hymenopteran and saproxylic insect assemblages in the canopy and understory of northern temperate forests

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Abstract: Insects respond to changes in microhabitat caused by canopy disturbance, and thus can be used to examine the ecological impacts of harvesting. Single-tree selection harvesting is the most common silvicultural system used to emulate local small-scale natural disturbance and maintain uneven-aged forest structure in temperate forests. Here, we test for differences in richness, abundance, and composition of hymenopteran and saproxylic insect assemblages at four different taxon levels (selected insect orders; and all hymenopteran families, and braconid subfamilies and morphospecies) between the canopy and understory of unharvested and single-tree selection harvested sites in a northern temperate forest from central Canada. Harvesting had no effect on insect assemblage richness, composition or abundance at the three highest taxon levels (order, family and subfamily). Similarly, richness and abundance at the lowest-taxon level (braconid morphospecies) were similar, although composition differed slightly between unharvested and harvested stands. Insect assemblages were vertically stratified, with generally higher abundance (for Diptera, Hymenoptera, some hymenopteran families and braconid subfamilies) and richness (for braconid morphospecies) in the understory than the canopy. In particular, composition of the braconid morphospecies assemblage showed relatively low similarity between the understory and canopy. Single-tree selection harvesting appears to influ-

ence wood-associated insect taxa only subtly through small changes in community composition at the lowest taxon level, and thus is recommended as a conservative approach for managing these northern temperate forests.

Keywords: selection harvesting; insect communities; canopy insects; Jack pine forests; forest management; high-taxon level; insect conservation

Introduction

Many insects respond to environmental changes caused by forest and canopy disturbance, and thus can be used as indicators of forest ecosystem health under varying management regimes (Niemelä 1997; Hammond et al. 2001; Pohl et al. 2007; Maleque et al. 2009). Selection (either single-tree or group) silvicultural systems, used traditionally in both tropical and temperate forests, create openings through tree removal and lead to uneven-aged, species-rich stands. By leaving much of the low-grade trees and branches on-site, they also provide a constant source of woody material that decays through time on the forest floor and acts as a nurse-bed to a wide range of saproxylic organisms. Many insect groups play key roles in forest ecosystems; however, studies on insect responses to selection cutting in northern temperate forests are limited focusing primarily on carabid beetles (Ulyshen et al. 2006, and references therein); other ecologically important insect groups, such as saproxylic insects and hymenopteran parasitoids, have been neglected.

Studies in temperate forests show that both hymenopteran (Deans et al. 2005) and saproxylic (Bouget 2005; Müller et al. 2007) insects are sensitive to forest harvesting and gap formation. Hymenopterans, in particular, have high diversity and play key roles in ecosystem functioning, including pollination, herbivory, predation, nutrient-cycling and parasitism. The largest group in this order, the superfamily of parasitoid wasps, which includes

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major families such as Braconidae, Ichneumonidae, and Chalcidoidea (Wharton 1993), are particularly sensitive to habitat change due to their high degree of specialization and upper position in trophic webs (LaSalle and Gauld 1993; Shaw and Hochberg 2001). The dipteran family Tachinidae, a large parasitoid taxon of forest insects residing outside the order Hymenoptera, has also been shown to respond to forest harvesting (Deans et al. 2005). Both of these parasitoid groups form diverse, complex food webs with wood-inhabiting or saproxylic insects, and have been shown to be indicators in either boreal (for dipterans including Dolichopodidae, Syrphidae, and Mycetophilidae; Deans et al. 2005; Makino et al. 2006) or temperate (for coleopterans including Scolytidae, Cerambycidae, Curculionidae, and Staphylinidae; Huhta et al. 1967; Pohl et al. 2007; Niklas and Götmark 2008) forests.

Selection harvesting, of either single trees or groups of trees, is repeated over long periods to ensure a continuous supply of diverse, high-quality hardwood forest products. These periodic harvests attempt to emulate local-scale natural disturbances, such as tree falls or wind damage, by creating forest gaps that open up the stand for regeneration (Smith et al. 1997) and change environmental conditions (Beaudet and Messier 2002). Selection harvesting has been equated with the removal of only valuable single-tree species (so called ‘high-grading’), but under the current standards of sustainable forest management (i.e. Forest Stewardship Council (FSC) certification) it also encompasses the cutting of less valuable trees (i.e. ‘low-grading’) in order to improve stand structure and species diversity in addition to long-term wood quality and supply. The selection silvicultural system is recommended for the management of northern deciduous forests (Nyland 1987), and is considered to maximize the production of high-quality products with relatively low environmental impact (OMNR 1998). Yet, little is known about the effects of selection harvesting on native animal communities, either vertebrates (e.g., Thompson et al. 1995; Menzel et al. 2002; Doyon et al. 2005) or invertebrates (e.g., Vance and Nol 2003; Moore et al. 2004). Animal assemblages play different roles in the functioning of forest ecosystems and some groups are important indicators of forest health in stands that are managed sustainably for a range of benefits. Here, we compare insect communities between unharvested sites and sites under low-grading single-tree selection cutting to understand the effects of this harvesting system on natural communities and make sustainable management recommendations that will maintain biodiversity in northern temperate forests.

Environmental and biological variability from the understory to the canopy appears to influence the vertical distribution of insect fauna in forested ecosystems (Basset et al. 2003). Such work is limited; however, to a few insect groups and results are inconsistent in terms of the differences in species richness and composition between the canopy and understory. In tropical forests, insects can be more diverse in the canopy (e.g. herbivore, Basset et al. 2001) or in the understory (e.g. flying insects, De Dijn 2003), or diversity can be similar in both vegetation strata (DeVries et al. 1997; Basset et al. 2001). The general pattern seems to indicate that sessile homopterans and formicids, unlike

most actively flying insects, will be richer and more abundant in the canopies of tropical trees than in their understories (De Dijn 2003). In northern temperate forests, vertical stratification of insects has been reported for herbivore assemblages using branch sampling (e.g., Le Corf and Marquis 1999). Similarly, in the first study to sample insects with Malaise traps in temperate forest canopies, differences were found between the canopy and understory in richness, abundance or composition of hymenopteran families, mymarid genera, and cerambycid species (Vance et al. 2003, 2007). Here, we examine the richness, abundance, and composition of selected insect groups in the canopy and understory of unharvested and selection-harvested forests to test whether single-tree selection harvesting will be a factor in insect vertical distribution. We focus on selected saproxylic assemblages and their associated predaceous and parasitic families at four taxon levels (order, hymenopteran family, braconid subfamily, and braconid morphospecies) in order to assess their comparative sensitivity to forest change and to better understand the impact of single-tree selection harvesting on insect biodiversity.

Materials and methods

Study design

To analyze differences in insect species richness and abundance between harvesting treatments, vegetation strata and their interactions, we used ANOVA in a split block design with three sites as blocks, harvesting treatment as the main factor and vegetation strata as the split factor. In each site, we selected an unharvested and a harvested stand (the harvesting treatment in the split block design). In each of the selected harvested and unharvested stands, two sampling stations were established at least 50-m apart. Data from different sampling stations were considered independent observations, because we assumed that the operation of traps from a sampling station will not influence the capture in traps at the other sampling station. At each sampling station, insects were collected in the canopy and in the understory; thus, vegetation stratum was the split factor in the design.

The statistical general model of a split block design is of the form

$$Y_{ijk} = \mu + r_i + \alpha_i + e_{ij} + \beta_k + e_{ik} + (\alpha\beta)_{ik} + e_{ijk} \quad (1)$$

with $i = 1, 2, \dots, n$; $j = 1, 2, \dots, a$ (row, the main factor or harvesting treatment); $k = 1, 2, \dots, b$ (column, the split factor or vegetation stratum). Here, Y_{ijk} is an observation, μ is the general mean, r_i are the block effects, α_i are the row and β_k the column effects, whereas $(\alpha\beta)_{ik}$ are the measures of interaction between rows and columns. e_{ij} , e_{ik} and e_{ijk} are the errors of the row, column and interaction, respectively. It tests the null hypotheses that there is no effect of the harvesting treatment ($\alpha_1 = \alpha_2 = 0$) or vegetation stratum ($\beta_1 = \beta_2 = 0$) on the insect assem-

blage, and there is no interaction between both $((\alpha\beta)_{jk} = 0$ for all j and k).

Study site and stand characteristics

The study was conducted at the Haliburton Forest and Wildlife Reserve (45°15' N, 78°35' W) located within the Algonquin Park Site District (5E9 for Hills 1959), in the Great Lakes-St Lawrence forest region of central Ontario, Canada. The region is primarily upland characterized by temperate, mixedwood (coniferous-deciduous) forests. Tolerant hardwood species such as Sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.) and Yellow birch (*Betula alleghaniensis* Britton) are the dominant trees, while White pine (*Pinus strobus* L.) is the characteristic conifer of the region.

The study area is managed under an uneven-aged selection silvicultural system, with both single-tree and group selection techniques conducted at short intervals (10–20 years). During the 1950's–1970's, selection harvesting high-grading resulted in the overexploitation of these forests. However, under the FSC certification, selection harvesting low-grading has taken place since the 1980's where less valuable trees have also been removed

while retaining a residual basal area from 16–18 m²/ha (P. Schleifenbaum, Haliburton Forest, Ontario).

All sites were dominated by Sugar maple. The unharvested stands had not been logged since 1940 whereas the harvested stands underwent low-grading single-tree selection harvesting (involving sugar maple removal in the previous 5 years) from 1996–2000. We have no records prior to 1940, but presume some white pine could have been removed by selective cutting although no stumps were found.

Diameter at breast height (DBH), sapling density (<5 cm DBH), and canopy cover were estimated at each sampling station. A basal area sweep using a prism with a basal area factor of 2 was carried out to identify trees with DBH ≥ 6 cm in variable-radius plots; thus, a total number of 154 trees were flagged, identified and the DBH measured (Table 1). Those trees also served to estimate stand composition. At each sampling station, sixteen 2-m² quadrats were established (one in each cardinal direction at 2, 4, 8, and 16 m from the center) and saplings (trees with DBH 1.00 to 5.99 cm) were identified and counted; sapling density was estimated at each stand (Table 1). A densiometer was used to measure canopy openness at the same positions as the quadrats were set.

Table 1. Diameter at breast height (DBH), the number of trees measured, sapling density (<5 cm DBH), canopy cover, and stand composition (percentage number of individuals) of trees with DBH ≥ 6 cm and of saplings in unharvested and selection cut stands at three deciduous forest sites in central Ontario, Canada.

Forest site		Average DBH (cm)	Number of trees meas- ured	Sapling density (no./m ²)	Total number of saplings counted	Canopy cover (%)	Stand composition (DBH ≥ 6cm) (%)					
							Sugar maple	Cedar	Ironwood	Paper birch	Beech	Yellow birch
Site 1	Unharvested	43.27	20	0.75	12	94.6	60	10	15	5	5	5
	Harvested	34.41	22	0.75	12	90.5	31.8				27.3	27.3
Site 2	Unharvested	39.38	36	1.25	19	98.1	58.3			5.5		2.8
	Harvested	33.91	27	0.5	4	95.4	74.1					18.5
Site 3	Unharvested	34.92	28	0.06	1	95.7	89.3				3.6	
	Harvested	35.45	-21	0.1	2	90.3	71.4		4.8		9.5	

Forest site		Stand composition (DBH ≥ 6cm) (%)				Stand composition (saplings) (%)						
		Balsam fir	Basswood	Hemlock	Red nagle	Sugar maple	Balsam fir	Red maple	Beech	Striped maple	Basswood	Yellow birch
Site 1	Unharvested					50	33.3	16.7				
	Harvested	13.6				16.7	41.6	25	16.7			
Site 2	Unharvested		27.3	2.8	2.8	84.2	10.5			5.3		
	Harvested		3.7	3.7		25	25			25	25	
Site 3	Unharvested		3.6	3.6					100			
	Harvested			14.3		50						50

Sugar maple (*Acer saccharum*), Cedar (*Thuja occidentalis*), Ironwood (*Carpinus caroliniana*), Paper birch (*Betula papyrifera*), Beech (*Fagus grandifolia*), Yellow birch (*Betula alleghaniensis*), Balsam fir (*Abies balsamea*), Basswood (*Tilia americana*), Hemlock (*Tsuga canadensis*), Red nagle (*Acer rubrum*), Striped maple (*Acer pensylvanicum*)

Insect sampling and identification

Two insect traps were set in each sampling station, one in the canopy and the other in the understory. We used modified Malaise traps recommended for sampling forest canopies (Finnamore

et al. 1998; Vance et al. 2003), each which had an intersecting surface of 6.7 m². Each trap collected insects into two bottles (one located at the top and the other at the bottom of the trap) containing 20%-ethanol glycol to kill and preserve insects. We used two sample bottles per trap because many taxa are collected

in either the top or the bottom bottle (Vance et al. 2007). Insects were sampled over 14 consecutive days in June, July and August 2003.

All captured Hymenoptera were identified to family following published identification guides (Goulet and Huber 1993; Grissell and Schauff 1990); and members of the Braconidae were identified to subfamily, genus in some cases, and morphospecies (Wharton et al. 1997). Selected saproxylic dipteran (Dolichopodidae, Mycetophilidae, Syrphidae, and Tachinidae) and colepteran (Cerambycidae, Curculionidae, Scolytidae, Staphylinidae) families were also identified using identification manuals, keys and guides (McAlpine et al. 1981, 1987; Oosterbroek 1998; White 1983; Klimaszewski and Watt 1997) to provide information on forest sensitive species.

Data analysis

Abundance was estimated as the number of individuals caught per trap during the 14 days, averaged over the three sampling periods to provide a good representation of the central tendency and variation of each trap capture during the whole summer. Data were also averaged for sampling stations in the ANOVA analysis, but considered as independent observations for the multivariate analysis. Many taxa were represented by very few individuals (rare taxa); thus, the criteria used to run the ANOVA on a given taxon were to be present in all three sampling periods and to have more than 15 individuals as the total caught. Data were transformed when necessary to meet the assumption of normality. The ANOVA analysis (split-block design) was run using SPSS PASW Statistics 17.0 (release 17.0.2), GLM Univariate, Method SSTYPE (3) which calculates the sum of squares of an effect F in the design as the sum of squares adjusted for any other effects that do not contain it, and orthogonal to any effects (if any) that does contain it. The Type III sums of squares have the major advantage of being invariant with respect to the cell frequencies as long as the general form of estimation remains constant. To examine differences in richness, the ANOVA analysis was conducted on the number of taxa caught in the Malaise traps. Because we had different abundances and only two samples per site and treatment, the Chao 1 estimator of species richness was calculated (EstimateS 7.5) for the canopy and understory of unharvested and harvested stands pooling data from the three sites. Correspondence Analysis (CA) (CANOCO version 4.5, ter Braak and Šmilauer 1998) was used to explore further differences in the selected insect families and braconid morphospecies by treatment and forest stratum.

To compare community composition between harvesting treatments or vegetation strata, we pooled data from the three sites and estimated Jaccard's similarity index (Koleff et al. 2003) for hymenopteran families, braconid subfamilies, and morphospecies between unharvested and harvested plots and between the understory and canopy. This index varies from 0 (no taxa are shared by both communities) to 1 (when all taxa are shared by both communities), and high values indicate high similarity between communities (or low β -diversity).

Results

Overall richness, abundance and composition

All sites were dominated by sugar maple and regeneration (as judged by sapling density) was relatively low (Table 1). Although canopy cover was close to 100% in all stands, it was significantly higher in unharvested than in harvested stands ($F = 24.807$, $p = 0.035$) (Table 1). There were no significant differences in DBH ($F = 2.807$, $p = 0.236$) or sapling density ($F = 0.779$, $p = 0.470$) between unharvested and tree-selection harvested stands. No differences were found by site in any of the insect community attributes and taxa, except for the abundance of one microgastrinid morphospecies.

A total of 1,885 hymenopterans representing 38 families were caught in the Malaise traps. Twelve of the hymenopteran families (Table 2) met the criteria to run the ANOVA analysis and test for differences between harvesting treatments and vegetation strata. Other families trapped (the total number of individuals caught in brackets) included: Trichogrammatidae (42), Ibalidae (14), Pteromalidae (11), Tenthredinidae (11), Xiphydriidae (11, mostly in the canopy), Aphelinidae (9), Cynipidae (9), Crabronidae (7), Dryinidae (7), Vespidae (6), Eucilidae (5), Pemphredonidae (5), Ampulicidae (2), Apoidea (2), Gasteruptionidae (2), Megaspilidae (2), Tiphidae (2), Torymidae (2), Argidae (1), Bethyidae (1), Chiripidae (1), Diprionidae (1), Embolemidae (1), Heluridae (1), Pergidae (1), Perilampidae (1), Proctotrupidae (1), and Siricidae (1).

The 425 individual braconids caught in the study period represented 17 subfamilies and 110 morphospecies. The ANOVA was run on the abundance of five subfamilies and six morphospecies (four from the Microgastrinae and two from the Euphorinae subfamily) (Table 3). Subfamilies caught at low numbers by the trapping system included: Alysiinae (14 individuals from the *Paroligoneurus*, *Dinotrema*, *Chorebus*, *Aphaereta*, *Orthostigma*, *Aspilota*, and *Phaenocarpa* genera), Doryctinae (6 individuals from *Heterospilus*, *Leluthia* and *Guaygata*), Braconinae (5 from *Hemibracon*, *Atanycolus* and *Bracon*), Opiinae (3 from *Opius* and *Exodontiella*), Hormiinae (4 from *Colastes*, *Lysitermus*, *Shawiana*, and *Parahormius*), Agathidinae (2 *Bassus* spp.), Homolobinae (1 *Charmon* spp.), Macrocentrinae (10 *Macrocentrus* spp.), Orgilinae (2 *Orgilus* spp.) and Blacinae (1 *Blacus* spp.). Many morphospecies were caught in only one month (26 in June, 31 in July and 23 in August), and most were caught in extremely low numbers such as one or two individuals.

Differences between unharvested and selection-harvested stands

Single-tree selection cutting showed no influence on the structure of selected insect assemblages at the high-taxa level. There were no significant differences between harvesting treatments in the total abundance of Hymenoptera ($F = 0.001$, $p = 0.984$), Diptera ($F = 0.003$, $p = 0.963$) and selected families of Diptera and Coleoptera (Table 2). The number of hymenopteran families caught

in the Malaise traps was similar among sites ($F = 0.174$, $p = 0.852$) and between unharvested and harvested stands ($F = 0.927$, $p = 0.437$) (Table 2). Confidence intervals of the estimated Chao 1 greatly overlapped between unharvested and harvested stands in the canopy (unharvested: 28 [20–72]; harvested: 24 [23–33]) as well as in the understory (unharvested: 42 [34–75]; harvested: 31 [27–53]), indicating similar family richness between treatments. The number of trapped braconid subfamilies (Table 3) was also similar among sites ($F = 2.554$, $p = 0.119$) and between harvesting treatments ($F = 2.649$, $p = 0.13$). No hymenopteran

family (Table 2) or braconid subfamily (Table 3) showed significant differences in abundance between unharvested and harvested stands. The Jaccard index indicated relatively high similarity in the composition of hymenopteran families (67.5%) and braconid subfamilies (76.5%) between unharvested and harvested stands (Table 4). The axes of the CA gave eigenvalues of 0.108 (axis 1) and 0.085 (axis 2) and the first two axes accounted for 46.6% of the variance. There was no clear separation between unharvested (open symbols) and selection-harvested (filled symbols) stands (Fig. 1), similar to that seen with the ANOVA.

Table 2. Mean number of individuals (per trap in 14 days, average over June, July and August) from selected insect families caught in the canopy (C) and understory (U) of unharvested and selection-harvested plots at three deciduous forest sites in central Ontario, Canada.

	Site 1 (Moose)				Site 2 (Marsh)				Site 3 (MacDonald)				<i>p</i> values ²	
	Unharvested		Harvested		Unharvested		Harvested		Unharvested		Harvested			
	C	U	C	U	C	U	C	U	C	U	C	U	Harvesting	Strata
Hymenoptera														
Braconidae	1.50	4.17	4.67	6.50	3.17	11.50	8.33	7.50	1.17	17.00	1.00	7.50	ns	0.014
Ceraphronidae	0	0.83	0.17	0.83	0	0.83	0	0.67	0	1.17	0.17	1.33	ns	<0.001
Chrysididae	0	0.67	2.17	0.17	0	0.17	0.67	0	1.83	0.33	1.33	0.33	ns	ns
Diapriidae	0	3.83	0.17	1.83	0.17	9.17	0.33	0.33	0	7.67	0	3.00	ns	0.03
Encyrtidae	1.5	0.33	0.67	1.17	1.67	2.83	0.83	0.50	0.33	0.16	0.33	4.33	ns	ns
Eulophidae	0.33	0	0.33	0.50	1.33	0.67	1.17	0.50	1.17	1.17	1.00	0.83	ns	ns
Formicidae	0.50	0	0.67	3.17	0.33	0.50	1.17	0.67	0.33	0.33	0.67	0.67	ns	ns
Ichneumonidae	1.33	9.00	3.17	9.50	1.83	14.00	7.16	3.67	1.83	23.67	0.83	11.50	ns	0.055
Mymaridae	0.67	3.17	2.50	2.00	1.33	4.17	2.00	1.00	1.17	4.50	2.00	5.17	ns	ns
Platygastridae	0.33	0.33	0	0.83	0.17	1.00	0	0.17	0.17	2.83	0	0.50	ns	ns
Pompilidae	0	0	0.17	0	0	0	0.83	0	0.33	0.33	0.50	0.67	ns	ns
Scelionidae	0.17	1.17	0.50	0.83	0.50	9.16	0	3.17	0.33	0.33	0.67	0.17	ns	0.001
Total abundance ¹	8.50	27.33	17.33	29.67	10.50	58.83	23.83	19.83	9.33	66.33	9.67	39.33	ns	0.038
No. families caught	13	11	20	20	9	24	17	14	13	24	15	19	ns	ns
Selected Diptera														
Dolichopodidae	3.67	8.33	8.33	8.67	8.17	8.50	10.33	4.67	7.00	11.33	8.67	8.50	ns	ns
Mycetophilidae	2.33	22.67	4.67	18.50	3.50	31.33	5.67	7.33	2.17	39.67	2.83	16.17	ns	0.009
Syrphidae	0.50	2.83	0.83	6.17	0.17	3.50	1.33	2.50	0.50	3.00	0.33	3.50	ns	0.040
Tachinidae	1.00	3.00	5.00	6.00	0.67	2.00	1.00	3.17	0.83	2.83	0.83	3.83	ns	0.034
Selected Coleoptera														
Cerambycidae	2.50	3.17	2.33	2.00	1.17	2.33	3.50	1.83	1.33	3.17	2.50	2.67	ns	ns
Curculionidae	66.17	137.67	24.50	39.67	40.33	122.0	40.00	49.17	13.17	104.17	26.00	68.50	ns	0.018
Scolytidae	6.67	1.83	6.67	2.83	2.50	1.17	1.67	2.17	2.67	1.00	1.83	1.33	ns	0.012
Staphylinidae	0.50	5.50	1.67	6.50	1.83	3.50	0.50	2.33	2.00	10.33	1.00	2.67	ns	0.027

¹ Includes rare (less than 15 individuals caught) families not listed here; ² Only significant ($p < 0.05$) values are shown

Composition at the low-taxon level was the strongest of the studied attributes to show differences between unharvested and selection-harvested stands. There was no significant difference in the number of morphospecies caught by site ($F = 10.108$, $p = 0.090$) or harvesting treatment ($F = 1.170$, $p = 0.392$) (Table 3). The Chao 1 estimation of morphospecies richness was much higher than the actual number caught in traps, indicating that even higher species richness is expected with increasing sample size. Confident limits of the estimated number of morphospecies highly overlapped in both the canopy and understory between harvesting treatments (unharvested-canopy: 67 [35–179]; unharvested-understory: 200 [121–390]; harvested-canopy: 67

[45–130]; harvested-understory: 96 [64–182]. Most morphospecies were represented by a single individual, and there was no significant difference between unharvested and harvested stands in the abundance of the most common morphospecies of Microgastrinae and Euphorinae (Table 3). The Jaccard index (25.2%) indicates low similarity in the braconid assemblages between the unharvested and harvested sites (Table 4). The first (eigenvalue 0.400) and second (0.360) axes of the CA accounted for only 27.6% of the variance and there was no clear separation in samples from unharvested and harvested stands (Fig. 2).

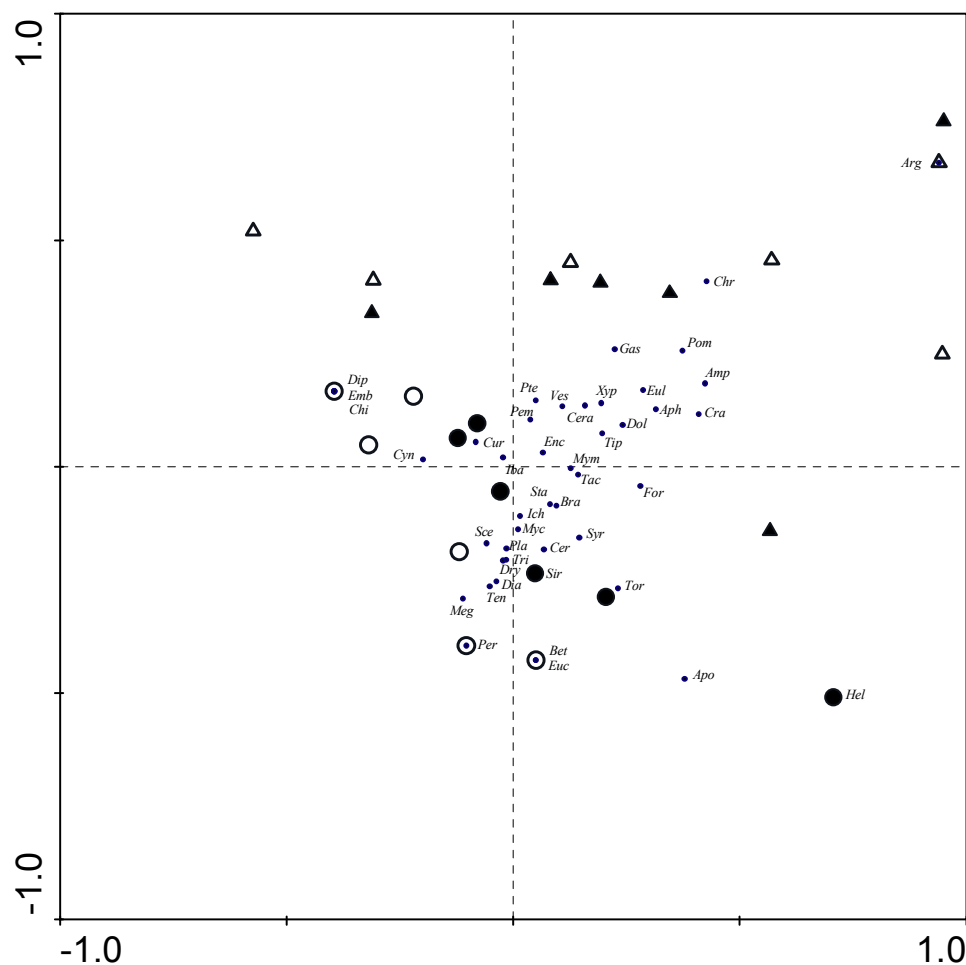


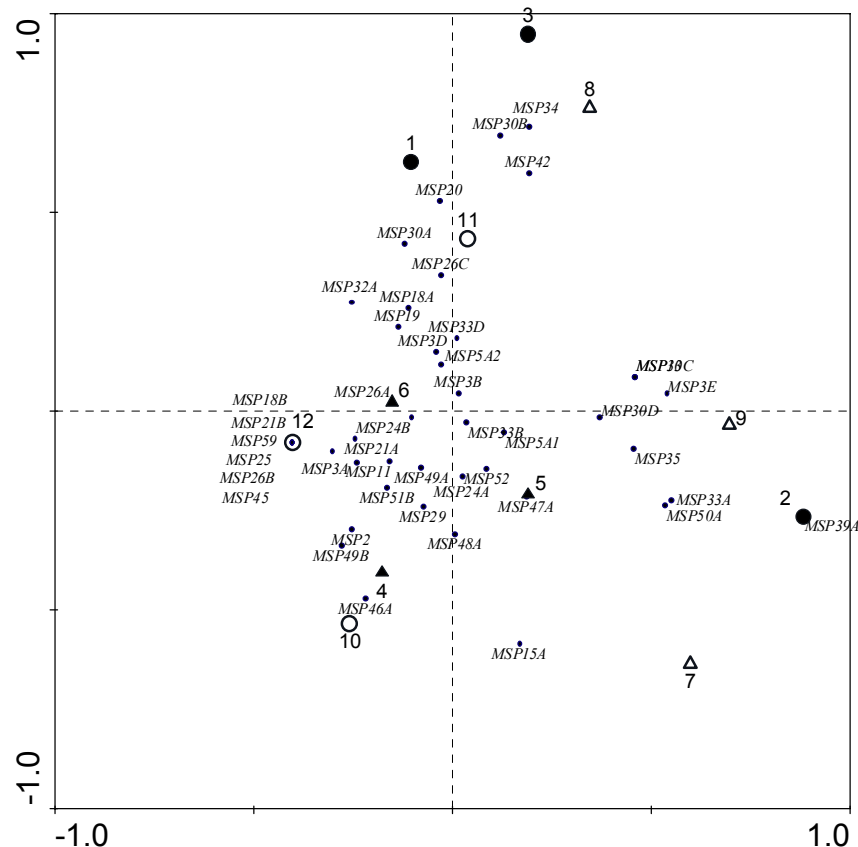
Fig. 1. Correspondence analysis of insect families (all hymenopteran and selected dipteran and coleopteran families) caught in Malaise traps in the canopy (triangles) and understory (circle) of unharvested (empty dots) and single-tree selection harvested (filled dots) stands in northern temperate forests of Ontario, Canada.

Table 3. Mean number of individuals (per trap in 14 days, average over June, July and August) from braconid subfamilies and morphospecies (Msp) caught in the canopy (C) and understory (U) of unharvested and selection-harvested plots at three deciduous forest sites in central Ontario, Canada.

	Site 1 (Moose)				Site 2 (Marsh)				Site 3 (MacDonald)				<i>p</i> values ¹		
	Unharvested		Harvested		Unharvested		Harvested		Unharvested		Harvested				
	C	U	C	U	C	U	C	U	C	U	C	U	Harvesting	Strata	Site
Aphidiinae	0.17	0.50	0.33	0.17	0.17	1.17	0.83	0.33	0.33	1.00	0	0.67	ns	0.030	ns
Meteorinae	0.33	0.33	0.17	0.33	0.17	0	0.50	1.00	1.00	1.33	0	0.33	ns	ns	ns
Cheloninae	0.33	0.17	1.00	0.33	0.83	0.33	3.17	1.17	0.17	1.50	0	1.33	ns	ns	ns
Microgastrinae	0.33	2.50	1.83	2.50	1.00	5.83	1.33	2.33	2.33	5.83	0.67	3.17	ns	<0.001	ns
Msp MIC2	0	0.83	0.17	0.17	0	0	0	0.17	0	1.17	0.17	0.67	ns	0.013	ns
Msp MIC 3A	0	0.67	0.17	0.67	0	0.83	0	0.17	0	2.00	0	0.50	ns	0.003	ns
Msp MIC 3B	0.17	0.67	1.17	1.17	0.17	4.17	1.00	1.83	0.50	1.83	0	1.83	ns	<0.001	0.039
Msp MIC 3D	0.17	0	0.17	0	0.83	0.33	0.17	0	1.50	0.17	0.50	0	ns	ns	ns
Euphorinae	0.17	0.67	0.17	0.50	0.50	0.83	0.50	1.17	0.17	2.00	0.33	0.67	ns	0.005	ns
Msp EUP 5A1	0.17	0.33	0	0.33	0.17	0.17	0.33	0.67	0.17	0.33	0.33	0.17	ns	ns	ns
Msp EUP 5A2	0	0.33	0.17	0.17	0.33	0.67	0.17	0.33	0	1.17	0	0.33	ns	0.002	ns
No. subfam caught	6	7	11	10	8	10	9	11	5	14	4	8	ns	0.004	ns
No. morphospecies	8	19	16	22	16	24	21	28	4	40	5	20	ns	0.015	ns

Table 4. The number of exclusive taxa and the Jaccard index of similarity for hymenopteran families and braconid morphospecies between harvesting treatments and vertical strata in three deciduous forest sites from central Ontario, Canada.

	Harvesting treatment			Vertical strata			Total number of taxa
	No. of taxa caught exclusively in unharvested stands	No. of taxa caught exclusively in harvested stands	Jaccard index	No. of taxa caught exclusively in the canopy	No. of taxa caught exclusively in the understory	Jaccard index	
Hymenopteran families	4	9	0.675	3	11	0.65	40
Braconid subfamilies	1	3	0.765	2	2	0.765	17
Braconid morphospecies	45	38	0.252	19	67	0.225	110

**Fig. 2.** Correspondence analysis of braconid morphospecies caught in Malaise traps in the canopy (triangles) and understory (circle) of unharvested (empty dots) and single-tree selection harvested (filled dots) stands in northern temperate forests of Ontario, Canada.

Differences between the canopy and understory

The studied insect assemblages showed some differences between the canopy and understory at the high-taxon level. More Hymenoptera ($F = 24.727$, $p = 0.038$) and Diptera ($F = 132.907$, $p = 0.007$) were caught in the understory than in the canopy (Table 2). Of the selected dipteran and colepteran families, Mycetophilidae ($F = 108.630$, $p = 0.009$), Syrphidae ($F = 23.678$, $p = 0.040$), Tachinidae ($F = 28.057$, $p = 0.034$), Curculionidae ($F = 55.284$, $p = 0.018$), Scolytidae ($F = 81.780$, $p = 0.012$) and Staphylinidae ($F = 36.144$, $p = 0.027$) were more abundant in the understory than in the canopy (Table 2); only Dolichopodidae (Diptera) and Cerambycidae (Coleoptera) did not show differences by forest strata. The number of hymenopteran families

caught in the Malaise traps was similar between the canopy and the understory ($F = 2.392$, $p = 0.262$). Although the Chao 1 estimation of richness was higher in the understory than in the canopy of both unharvested and harvested stands, confident intervals overlapped greatly (see above). The understory was richer on braconid subfamilies than the canopy ($F = 12.162$, $p = 0.004$). Braconidae ($F = 70.642$, $p = 0.014$), Diapriidae ($F = 32.392$, $p = 0.030$), Ichneumonidae ($F = 16.651$, $p = 0.055$), and the braconid subfamilies Aphidiinae ($F = 6.081$, $p = 0.03$), Microgastrinae ($F = 19.074$, $p < 0.001$) and Euphorinae ($F = 12.000$, $p = 0.005$) were all more abundant in the understory than in the canopy (Tables 2 and 3). There was no significant interaction between site, harvesting treatment and vegetation stratum for any of the study taxa. The Jaccard index of similarity showed relatively high overlap in the composition of hymenopteran families (65%)

or braconid subfamilies (76.5%) between the understory and canopy (Table 4). In the CA biplot, canopy samples (triangles) were located in the upper side whereas understory samples (circles) were mainly in the central area (Fig. 1), reflecting some separation between the canopy and understory at the high-taxa level. Canopy samples from both unharvested (empty triangles) and harvested stands (filled triangles) showed a similar pattern along the first ordination axis, which is consistent with similarities in community structure at the family level observed between unharvested and harvested stands in the ANOVA. Understory samples (circles) also showed a similar pattern between unharvested and harvested stands, but the understory of harvested stands appeared to be associated with a large number of taxa.

The understory was richer in braconid morphospecies than the canopy ($F = 63.443$, $p = 0.015$) and most of the studied morphospecies were also more abundant in the understory (Table 3). The Chao 1 estimated higher species richness in the understory than in the canopy of both unharvested and harvested stands (see above). The Jaccard index for braconids comparing understory and canopy was low, indicating vertical stratification in the assemblage composition (Table 4). The CA biplot for braconid morphospecies showed no separation between the canopy and understory (Fig. 2).

Discussion

Despite detailed examination at four taxon levels, we found few differences in the richness and abundance of saproxylic insect assemblages between unharvested and single-tree selection harvested stands suggesting that such activity has little effect on their community structure. In temperate deciduous forests, understory regeneration results in rapid decreases in light availability following selection harvesting (Beaudet et al. 2004). If we consider harvesting in northern temperate forests over a gradient of environmental impact, we would expect single-tree selection cutting to have the lowest impact followed by group selection, strip selection, and finally clear-cutting (Siira-Pietikäinen et al. 2003). In northern temperate forests of Ontario, Nol et al. (2006) found more hoverflies (syrphids) and bees in sites recently harvested with the single-tree selection system than in sites unharvested at least for 40 years; in contrast, click beetles (Elaterids) were collected more often in old logged sites. In European boreal forests, Atlegrim and Sjöberg (1996) found the abundance of some herbivorous insect larvae to be lower in clear-cut areas than in selection harvested sites. Siira-Pietikäinen et al. (2003) showed that selection harvesting, unlike more intensive harvesting techniques, had no impact on functional (such as herbivores, predators, detritivores, fungivores) and taxonomic (species of Carabidae and Staphylinidae) arthropod assemblages in the boreal forest of Finland. Moore et al. (2004) reported no difference in carabid assemblages between group selective-cut and uncut sites, but did observe some differences in strip-cut sites in northern forests of Quebec. The single-tree selection cutting conducted in our study likely had less effect than typical selection harvesting systems because its objective was to conserve biodi-

versity as well as produce quality timber. Under such a scenario, fewer trees (many of low value often left on site) would have been cut and removed than in more product-oriented forests. The relative similarity in stand structural attributes we observed between treatments supports this interpretation.

Composition (hymenopteran families and braconid morphospecies) seemed to be more influenced by selection harvesting than other community attributes such as species richness or relative abundance. Of the insect taxa we studied, only composition of the braconid assemblage differed between unharvested and selection-cut stands. Few studies have examined the effects of selection harvesting on insects in temperate forests. Of these, ground-dwelling carabids have been the most common focal group showing varying sensitivity in all three community attributes depending on taxon level and stand characteristics (time since harvest, size of gaps, and intensity of cutting). Moore et al. (2004) reported no effect on any community attribute for carabid beetles 6–8 years after selective cutting (with small gaps) in northern hardwood forests of Quebec, while Werner and Raffa (2000) found species composition in carabid beetles to be the only attribute that differed between forest management regimes (including single-tree selection cutting) in the Great Lakes region. As we found with the braconid morphospecies, Ulyshen et al. (2006) similarly showed community composition of carabid beetles differed in old (cut seven years before) gaps from the surrounding stands in hardwood forests of the southeastern U.S. while abundance and richness remained the same (although higher in recent than old gaps). In contrast, Vance and Nol (2003) found both composition and abundance of carabids to be similar in old (cut 15–20 years before) tree-selection-cut and uncut forests in Ontario, although their abundance in young (cut 0.5–3 years before) single-tree selection sites was lower than in old cut sites. Our study, the first to examine the effects of harvesting on insect assemblages caught with Malaise traps while flying in the canopy and understory of temperate forests, showed that composition is the community attribute most sensitive to selection harvesting in these northern temperate forests.

Insect assemblages were distinctly different in the two vegetation strata (understory and canopy) that we examined at both the high- and low-taxa levels. Vertical stratification of insects has been better explored in tropical (Basset et al. 2003; De Djin 2003) than in northern forests especially with respect to insects captured flying in the canopy (see Lowman and Wittman 1996; Stork et al. 1997; Vance et al. 2007). Le Corf and Marquis (1999) observed that although the overall density of herbivores, species richness and species composition were similar between the canopy and understory in oak trees from Missouri, five herbivore families differed significantly between forest strata. We found that all selected saproxylic and dipteran families showed vertical stratification in their abundance except Dolichopodidae and Cerambycidae, the latter in contrast to Vance et al. (2003). In our study, the coleopterans Curculionidae and Staphylinidae and the dipterans Mycetophilidae, Syrphidae and Tachinidae were more abundant in the understory than in the canopy, with only Scolytidae showing the reverse pattern. Temperate forest canopies are exposed to harsh environments (high winds, intense temperature,

radiation, and rainfall) and many insect communities are found more commonly at lower levels (Lowman and Wittman 1996) or in the understory where survival is predicted to be higher, chemical cues from hosts better detected, and/or foraging easier than on top of the canopy.

In our study, a similar number of hymenopteran families were caught in the canopy and understory, and composition showed 65% similarity. In similar stands, rarefaction curves produced by Vance et al. (2007) predicted more hymenopteran families in the canopy than in the understory, with 73% similarity. At a lower taxon level, they also predicted more mymarid genera in the understory than in the canopy, which is similar to our findings with braconid morphospecies. Similarity in composition tends to decrease as lower taxon levels are considered, and the fact that many of our morphospecies were represented by a single individual would have certainly influenced these results. Yet, our 22% similarity between the canopy and understory in the braconid morphospecies assemblage was very close to that found for cerambycid species (21% by Vance et al. 2003), which were more abundant than our braconids. Braconids are a very rich taxonomic group, and consequently intensive sampling effort and systematic expertise are required to detect possible patterns or responses to environmental changes. Because many of the morphospecies we collected were only found during a single sampling period, future work should be conducted throughout the summer; if time is a constraint, then July should be the optimal month because this is when we observed the highest abundance and richness. Not surprisingly, braconid species diversity will also be best measured in the understory where plant species and structural diversity will enhance the likelihood of diversity in lepidopteran species that act as a host resource.

We used both high- and low-taxon levels to detect possible differences between selected insect communities after single-tree selection harvesting in northern temperate forests. An increasing number of studies emphasize the use of high-taxon levels or/and functional groups to monitor environmental changes in forest ecosystems because species identification can be untenable and/or very time-consuming, especially in highly diverse groups such as parasitoids (e.g. Williams and Gaston, 1994; Katzourakis et al. 2001; Bellocq and Smith, 2003). Williams and Gaston (1994) found that family richness was a good predictor of species richness in a variety of taxa including insects. In northern forest ecosystems, insects have been shown to respond to gradients of forest retention during harvesting at both high- and low-taxon levels (Siira-Pietikäinen et al. 2003; Deans et al. 2005, 2007). Our study lends further support to the use of higher taxon levels within forest management planning as this approach helps to rapidly identify areas of high insect diversity and conservation value while at the same time allowing for the necessary development of better taxonomic keys and expertise.

It appears then that single-tree selection harvesting carried out in these northern temperate forests has minimal structural effect immediately after cutting and will influence wood-associated insect taxa only through subtle changes in community composition. Although harvesting clearly leads to changes in understory development and light intensity, which in turn may account for

some of the minor compositional shifts we observed, the insect assemblages studied here displayed few responses to these effects within the first 3–5 years after cutting. Thus, our work provides support for single-tree selection harvesting as a management strategy to reduce impacts on diversity and help conserve the diversity of hymenopteran and wood-associated insect communities in these forests.

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